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ing functional FANCI-FANCD2, the level of –1 products did eventually decrease (Fig. 3, B and C, and fig. S8). However, since the extension products never accumulated to more than ~30% of the mock-depleted samples (Fig. 3D and fig. S8), we infer that this decline of –1 products is primarily due to degradation (*12*). We conclude that in the absence of FANCI-FANCD2, nucleotide insertion opposite the cross-linked base is inhibited. This differs from the effect of DNA polymerase ζ immunodepletion, which arrests lesion bypass immediately after the insertion step (fig. S9) (*12*).

We next investigated whether FANCI-FANCD2 is required for incisions, which are thought to occur on one of the parental strands on either side of the lesion (*2*) (Fig. 1A, ii). To visualize incisions, DNA repair intermediates were digested with Hinc II and analyzed by denaturing gel electrophoresis and Southern blotting (Fig. 4A). After 40 min, the most abundant species were the high-molecular-weight parental X-shaped molecules, as well as 2.3- and 3.3-kb species that represent stalled nascent strands (Fig. 4B, lane 4). Dual incisions surrounding the ICL are expected to convert the parental X-shaped molecule into a 5.6-kb linear product and 2.3- and 3.3-kb fragments (Fig. 4A). As expected, in mock-depleted extract, we observed a time-dependent decrease of X-shaped molecules and a concomitant increase in linear species (Fig. 4B, lanes 4 to 9; quantified in Fig. 4, C and D). The 2.3- and 3.3-kb species declined over time because of lesion bypass and/or resection (Fig. 4B). The kinetics of X-shaped molecule disappearance in this assay confirmed our previous conclusion (*12*) that the majority of incisions occurs after forks reach the –1 position (fig. S10C).

In the absence of FANCD2, incisions were severely inhibited, as seen from the persistence of X-shaped species and a severe delay in the accumulation of linear molecules (Fig. 4B, lanes 10 to 15; quantified in Fig. 4, C and D). In addition, the 2.3- and 3.3-kb fragments persisted longer, likely because of inhibition of lesion bypass. These effects were rescued by FANCI-FANCD2^{WT}. Tracking only the parental strands in this assay confirmed that incisions are inhibited in the absence of FANCD2 and showed that the defect is not rescued by FANCI-FANCD2^{K562R} (fig. S11). Together, these data show that ubiquitylated FANCI-FANCD2 is required for efficient incisions surrounding the cross-link.

Finally, we examined the precise timing of FANCI-FANCD2 ubiquitylation. As shown in fig. S12C, FANCI and FANCD2 ubiquitylation correlated with the arrival of leading strands at the –1 position, consistent with a role for the FANCI-FANCD2 complex in the insertion and incision steps, which occur after forks reach the –1 position (*12*) (figs. S10 and S12).

Using a chemically homogeneous cisplatin ICL and a bona fide repair assay, we show that the Fanconi anemia pathway is required for DNA replication–coupled ICL repair. These results explain why Fanconi anemia cells treated with ICL-inducing agents arrest late in S phase (*11*) and eventually die. We further demonstrate that FANCI-FANCD2 must be ubiquitylated to support repair, which suggests that its role in this process involves direct binding to the lesion. In the absence of FANCI-FANCD2, incisions near the ICL and translesion synthesis (TLS) past the lesion are severely inhibited, defining two critical steps in ICL repair that fail when the Fanconi anemia pathway is compromised. Although at present we cannot determine whether the insertion or incision steps occur first, it is widely envisioned that incisions must precede insertion (*2*). In this view, FANCI-FANCD2 might directly promote incisions and thereby affect TLS indirectly (fig. S13A). For example, FANCI-FANCD2, which contains no apparent nuclease domains, could promote dual incisions by recruiting the Slx4 nuclease complex to the lesion (*17*). However, we cannot rule out the converse scenario, in which TLS precedes incisions (fig. S13B), which would involve translesion DNA synthesis past an ICL (*18*). In this case, the primary function of FANCI-FANCD2 might be to promote TLS, perhaps via interaction with the ubiquitin-binding domains of Rev1. This model is consistent with genetic epistasis between TLS polymerases and the FA pathway (*19*), as well as reduced damage-dependent mutagenesis in FA cells (*20*). Finally, FANCI-FANCD2 might directly control both the incision and insertion steps (fig. S13C). Future experiments will be required to establish a molecular model of how FANCI-FANCD2 regulates the incision and/or TLS machineries during replication-coupled ICL repair.

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Indirect Punishment and Generosity Toward Strangers

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Many people incur costs to reward strangers who have been kind to others. Theoretical and experimental evidence suggests that such "indirect rewarding" sustains cooperation between unrelated humans. Its emergence is surprising, because rewarders incur costs but receive no immediate benefits. It can prevail in the long run only if rewarders earn higher payoffs than "defectors" who ignore strangers' kindness. We provide experimental evidence regarding the payoffs received by individuals who employ these and other strategies, such as "indirect punishment" by imposing costs on unkind strangers. We find that if unkind strangers cannot be punished, defection earns most. If they can be punished, however, then indirect rewarding earns most. Indirect punishment plays this important role, even if it gives a low payoff and is rarely implemented.

Indirect reciprocity is widespread in human societies. It occurs when we incur costs to reward those we know have been kind to others or punish those we know have been unkind to others. Indirect reciprocity is based on reputation and helps to enforce trustworthy behavior between individuals who do not know each other and who may not meet again. Such encounters form a substantial part of our interactions and are especially frequent in online commerce.

Indirect reciprocity is at work, for example, when someone financially supports anonymous volunteers working at food banks that help the poor, even though this person does not face the risk of ever needing a food bank's services. The donor's helping behavior is, therefore, called indirect rewarding. Such costly indirect rewarding is thought to be a key factor in the evolution of human cooperation (*1*–*4*). Experimental research (*5*–*8*) and theoretical considerations (*9*–*11*) suggest that indirect rewarding can sustain cooperation among unrelated humans. However, there is little empirical evidence about the long-term performance of indirect rewarding itself. People who engage in costly rewarding may lose out in the long run against "defectors" who never reward and thus avoid the associated costs. Even if good reputation is rewarded (*12*), indirect rewarders might lose out against "cautious defectors" who are generous only to avoid a bad reputation.

Indirect reciprocity may also take the form of costly indirect punishment. Though punishment has been observed to be important for promoting cooperative behavior in direct encounters (*13*), recent theoretical work suggests that it may be only marginally relevant when interaction is indirect (*14*). Empirical evidence on the use of indirect punishment and its long-term performance is missing, however.

We provide experimental evidence of human behavior in an anonymous environment where individuals can indirectly reward and punish. We determine the occurrences of different types of behaviors, including indirect rewarding, indirect punishment, defection, and cautious defection, among human participants and determine their payoff performance.

Our experimental design builds on the so-called "indirect helping game" (*5*, *8*, *9*). In total, 140 participants are repeatedly (100 rounds), anonymously, and randomly matched into donor-recipient pairs. Because roles are determined randomly, participants will typically be the donor in approximately half of the rounds. In the indirect helping game, only donors make decisions. In any round, each donor first observes the recipient's recent behavior in the role of donor and then decides whether to "help" the recipient or to "pass." Helping is costly for the donor and beneficial for the recipient, with the benefits exceeding the costs. In earlier experiments, indirect punishment was not available as an option, a restriction that is arguably not a realistic feature of human interactions (*13*–*16*). In our experiment, the donor can choose to "hurt" the recipient instead of passing or helping. Hurting is costly for the donor, but we vary its impact on the receiver. We conducted two treatments that differ only in this impact, which allows us to isolate the effect of indirect punishment on the payoff performance of different types of behavior. In our main treatment [harmful punishment (HP)], a hurt recipient loses 250 units of our experimental money, "francs." In the control treatment [symbolic punishment (SP)], a hurt recipient loses or earns no francs. We say that punishment is harmful in HP but only symbolic in SP. In both treatments, the donor loses 50 francs for hurting or 200 francs for helping, and the recipient earns 250 francs when he or she receives help. Passing does not affect either player's payoff. In both treatments the recipient observes the donor's action. Treatment SP is a control for HP, because it identifies differences in behavior between environments where indirect punishment has material consequences for the recipient and where it does not, while holding all other parameters constant across treatments (*17*–*19*).

Before choosing an action, donors observe a part of their recipient's donating history. A donor always learns his or her recipient's three most recent actions (first-order information) and, for a small price, can access the first-order information their recipients observed when making these decisions (second-order information). For treatments HP and SP, we collected data for, respectively, 8 and 6 independent cohorts of 10 participants.

The aggregate frequency (60.7%) of helping choices in our experiment falls within the range (50 to 85%) observed in experiments without the option of indirect punishment (*5*, *8*). Comparing HP to SP surprisingly shows that, in spite of the possibility of imposing costs on uncooperative recipients in HP, the two treatments exhibit no significant differences in average helping rates. Donors choose help with 60.0% frequency, on average, across the six cohorts in SP and 61.2% frequency, on average, across the eight cohorts in HP. This difference is not significant ($z = -0.065$, $P = 0.95$, two-sided Mann-Whitney U test, $N =$ 14 cohorts). Because behavior in both treatments displays a pronounced endgame effect, we restrict our analysis to the first 90 rounds (*17*).

In SP, punishment is very rare (1.1%), which is not surprising because it is costly for the donor but only symbolic to the recipient. When punishment is harmful (HP), it is used significantly more often ($z = -2.207$, $P = 0.027$, two-sided Mann-Whitney U test, $N = 14$) but still infrequently (3.4%). In both treatments, donors typically reward kind behavior with helping. When the recipient's history reveals unkind behavior toward others, donors more often pass than hurt. This preference for passing may explain why the punishment option in HP fails to increase cooperation beyond levels obtained without an option to punish (*5*, *8*). The infrequent use of punishment in our indirect reciprocity game seems to contrast the experimental results from public goods games with direct punishment, where frequent punishment of defectors sustains cooperation in the short (*13*, *20*) and intermediate run (*21*). This difference in results might be driven by the structural differences between the games. In our indirect reciprocity game, each action is indirect and targeted at a single person. In contrast, only punishment can be targeted at a specific person in public goods games, whereas any other action affects every member of the group. In combination with the difference in parameters, this may explain the level of punishment we observe (*17*).

Recent evidence suggests that human reciprocity is driven to a large extent by stable behavioral strategies (*22*–*24*), and a rich set of such strategies has been identified in recent models of evolution of indirect reciprocity (*1*, *9*, *10*). We consider seven prominent behavioral strategies and assess their payoff performance. These strategies are partitioned along the different ways a donor may use his or her own history or that of the recipient when choosing an action (*10*).

The first partition distinguishes between "discriminate" and "indiscriminate" strategies. An indiscriminate strategy does not condition an action on the donor's or recipient's histories. For example, "indiscriminate altruism" always prescribes help, and "indiscriminate defection" always prescribes pass.

The second partition divides discriminate strategies into those with selfish concern ("self-regarding") and those with concern for others ("other-regarding"). The strategy "cautious defection" employs occasional helping to maintain the donor's good reputation. In particular, it prescribes to help only when the donor's own

Table 1. Strategies in the indirect reciprocity game with punishment. The percentages of individuals identified with a strategy are given in parentheses, with their percentage in SP shown first and their percentage in HP shown second.

	Self-regarding	Other-regarding			
Indiscriminate	Defectors (9.6%, 10.5%)	Altruists (7.7%, 9.2%)			
Discriminate	Cautious defectors (7.7%, 10.5%)	Rewarders		Punishers	
		Image (50.0%, 39.5%)	Standing (25.0%, 17.1%)	Image (0%, 5.3%)	Standing (0%, 7.9%)

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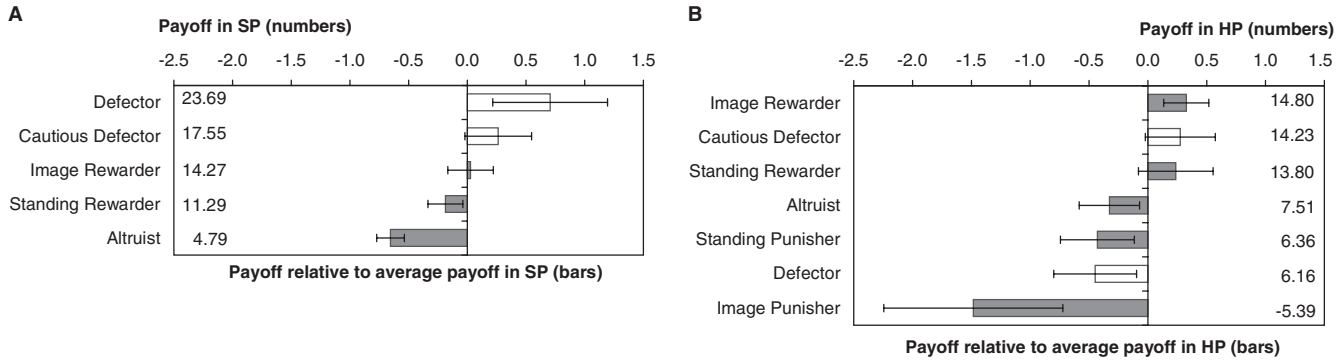

Fig. 1. Average and relative payoffs of the different strategies in SP (**A**) and in HP (**B**). Numbers inside the graph indicate average payoffs per round (in francs) of different strategies. Bars indicate the average payoffs of different strategies relative to the average payoffs across all participants in the respective treatment, and error bars indicate ±1 SE of these average relative payoffs. Tables S1 to S3 in the SOM (*17*) provide detailed information of payoffs for each strategy, cohort, and individual.

history shows little helping. Thus, it is discriminating and self-regarding (*10*).

Strategies that do condition actions on the recipient's history are discriminate and other-regarding. We focus on the "reciprocal" strategies that prescribe help only to those recipients whose history reveals frequent helping. The third partition divides the reciprocal strategies between "punishing" strategies that use the possibility to hurt unhelpful recipients and the "rewarding" strategies that do not.

The fourth partition divides the reciprocal strategies on the basis of the type and amount of information they use. This allows us to distinguish between standing and image scoring (*1*, *9*, *10*, *25*). An individual's "image score" and "standing" are statistics that summarize his or her reputation (*9*, *10*). A person's image score decreases when he or she passes and increases when he or she helps, whereas a person's standing decreases only when he or she passes on a recipient with a good reputation. An image-scoring strategy prescribes helping only those recipients with a high image score (*9*), and a standing strategy prescribes helping only those with high standing (*10*). Specifically, a standing strategy prescribes that a donor base his or her action not only on the first-order information about the recipient but also on the underlying second-order information. The latter indicates what the recipient knew about his or her recipient when choosing past actions as a donor. Using the combination of the final two partitions, we distinguish between "image rewarding," "image punishing," "standing rewarding," and "standing punishing." Because of the availability of hurting and the limits on the observable history in our experiment, we consider approximated standing and image-scoring strategies.

For each participant, we determine whether his or her actions across rounds 1 to 90 are consistent with any single behavioral strategy. Details and a graphic depiction of our classification procedure are provided in the supporting online material (SOM) (*17*). We refer to classified participants as rewarder, punisher, etc. Table 1 summarizes the identified strategies and shows for each the proportion of participants using that particular strategy. Almost all participants (SP: 86.7%; HP: 95.0%) can be classified. More classified participants use image-scoring strategies than standing strategies; among them, there are more rewarders than punishers. The next-largest fractions are those of indiscriminate and cautious defectors, with approximately half of them being cautious. The smallest group is formed by indiscriminate altruists.

Little is known about the payoff consequences of using various strategies in indirect reciprocity games (*12*, *26*). Such information is important because a strategy can flourish in the long run only if it yields a higher benefit than the alternatives. We consider the identified strategies and calculate the average cohort payoff generated by each of them (Fig. 1). For each participant, we calculate, in francs, the average earnings as a donor plus average earnings as a recipient across rounds 1 to 90. The payoff for a strategy is calculated for each cohort where the strategy is observed, as the average payoff across the participants using this strategy. These payoffs per cohort are used in our statistical analysis; however, it is the relative fitness of a strategy that determines its long-term success. Figure 1, therefore, shows for each treatment the average payoff of each strategy relative to the treatment average payoff. This relative payoff is calculated as [(average payoff of all participants in treatment using a particular strategy) – (average treatment payoff)]/(average treatment payoff).

Figure 1 reveals important payoff differences between the two treatments. In treatment SP, the indiscriminate defectors fare best (average payoff = 23.69 francs). Compared with the combined classes of defectors (20.96), the combined rewarders (13.28) earn significantly less ($P = 0.044$, two-sided Wilcoxon signed-ranks test, $N = 5$ paired observations); the altruists fare worst, and not only when compared with the defectors (4.79). Hence, defection outperforms all other strategies. In treatment HP, the payoffs are markedly different. The cautious defectors (14.23), image rewarders (14.80), and standing rewarders (13.80) are more successful than the indiscriminate defectors (6.16). Even if we combine the two classes of defectors (10.20), the combined rewarders (14.50) earn significantly more ($P = 0.068$, two-sided Wilcoxon signed-ranks test, $N = 8$ paired observations). Noticeably, the punishment strategies, which are used only in HP, are among the least successful (6.4).

The stark difference in the ranking of earnings across the two treatments is caused mainly by the distinctly lower earnings of indiscriminate defectors in HP, as compared with SP ($z = 1.715$, $P = 0.086$, two-sided Mann-Whitney U test, $N = 9$). This is a direct consequence of harmful punishment. The slightly higher punishment rate in HP (3.4%) than in SP (1.1%) is almost entirely directed toward defectors (SP: 1.6%; HP: 12.8%) ($z = 1.976$, $P = 0.048$, two-sided Mann-Whitney U test, $N = 9$) and cautious defectors (SP: 1.2%; HP: 5.2%) ($z = 1.375$, $P = 0.169$, two-sided Mann-Whitney U test, $N = 8$). Hence, though harmful punishment is rare, it substantially reduces defectors' earnings and changes the ranking of earnings among strategies.

Our results regarding the effects of indirect punishment complement recent experimental research showing that costly direct punishment may disfavor individuals and groups in repeated direct interactions with strangers, at least in the short run (*27*–*29*). However, our earnings comparisons across treatments reveal that, in indirect reciprocity games, punishment does not need to be frequent to promote the relative success of reward strategies. Theoretical models of indirect punishment investigating its long-term effects on cooperation are just starting to emerge (*14*). Our study can aid the development of such models by showing that indirect punishment, although rare, can support human cooperation.

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On the Origin of Species by Natural and Sexual Selection

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Ecological speciation is considered an adaptive response to selection for local adaptation. However, besides suitable ecological conditions, the process requires assortative mating to protect the nascent species from homogenization by gene flow. By means of a simple model, we demonstrate that disruptive ecological selection favors the evolution of sexual preferences for ornaments that signal local adaptation. Such preferences induce assortative mating with respect to ecological characters and enhance the strength of disruptive selection. Natural and sexual selection thus work in concert to achieve local adaptation and reproductive isolation, even in the presence of substantial gene flow. The resulting speciation process ensues without the divergence of mating preferences, avoiding problems that have plagued previous models of speciation by sexual selection.

Even as we commemorate the 150th anniversary of Darwin's *On the Origin of Species* (*1*), discussion continues on whether speciation is adaptive (that is, driven by selection) and to what extent it is inhibited by gene flow (*2*–*7*). Ecological conditions can induce natural selection for local adaptation (*2*, *8*), but disruptive or diversifying selection is usually not sufficient for speciation if individuals can migrate between habitats. In such cases, a mating structure has to emerge that strongly reduces hybridization between ecologically specialized populations (*3*–*5*).

Sexual selection is likely to play a pivotal role in shaping such a mating structure during incipient speciation (*9*) and has been suggested to induce speciation by causing the divergence of mating preferences between two emerging species (*9*–*13*). Yet speciation due to diverging mating traits is controversial, because existing theoretical models can explain the divergence of mating preferences only under conditions that are rarely met in nature (*10*, *13*, *14*). Moreover, the models tend to rely on Fisherian sexual selection to generate reproductive isolation. Fisher's runaway process of sexual selection involves preferences for arbitrary ornaments that reflect nothing but attractiveness (*15*). The runaway process could thus potentially evolve in different directions, allowing the divergence of preferences during speciation. However, mating preferences are generally not arbitrary but act on ornaments that indicate genetic or phenotypic quality (*15*–*17*), providing choosy individuals with either direct benefits or good genes for their offspring (*15*, *18*–*20*). The adaptive directionality of mate choice based on such indicator traits makes it difficult to conceive how this process could lead to the divergence of preferences between two nascent species.

By means of the following scenario, we will demonstrate that the divergence of mating preferences is not required for sexual selection to contribute to speciation. We consider a patchy environment that imposes contrasting selection pressures on an ecological character like a food-exploitation strategy (Fig. 1). We assume that across all habitats, intermediate ecological strategies, on average, do worse than specialist strategies optimizing the use of one of the habitats. Accordingly, natural selection is stabilizing within habitats but disruptive at the level of the entire population.

Individual-based computer simulations [based on Levene's "soft-selection" model (*21*), also see supporting online material (SOM)] that implement this ecological scenario highlight the overpowering effect of gene flow (Fig. 2A). Although disruptive selection removes individuals with intermediate phenotypes from the population, such individuals are created anew every generation as a result of migration between the habitats and recombination between different specialist genotypes. This process prevents the population from splitting into two locally adapted species, unless disruptive selection is unusually strong.

Having observed that ecological disruptive selection per se is not sufficient to result in speciation, we next consider an ornament, such as a plumage characteristic, that is expressed in a condition-dependent manner (*15*, *22*, *23*). Individuals adapted to the local environment are likely to be in a better condition, allowing them to develop brighter plumage than individuals that are less well adapted (*24*). Thus, by virtue of its condition-dependent expression, the ornament functions as an indicator for the degree of local adaptation (*25*–*27*).

Assuming that the ornament is expressed in males and that females are the choosy sex, one would expect females to evolve a preference for elaborate ornamentation, thereby using the information on local adaptation revealed by the male's ornament (*26*). Simulations that allow for the evolution of a preference and condition-dependent ornamentation [following (*17*); also see SOM] confirm this expectation (Fig. 2C). Starting from a randomly mating population ($p = t = 0$ at generation 0), female choosiness (p) evolved along with a concurrent increase in the resources invested by males in their ornament (t) to signal their ecological performance. The evolutionary process is driven by sexual selection and fueled by rare mutations introducing variation in female choosiness and male ornamentation. In our model, mating with a locally adapted partner is beneficial to a

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Indirect Punishment and Generosity Toward Strangers

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Cheaper Cooperation

In the context of public goods games in which optimal benefit is achieved when all participants contribute, bad behavior cannot always be deterred by direct punishment, and has the added disadvantage that the punisher may suffer a cost. Alternatively, instead of punishment, rewarding those who contribute can be effective in encouraging and maintaining widespread cooperation, with the added plus that group benefits are not diminished by the costs of punishment. But Ule *et al.* (p. 1701) discovered experimentally that if someone is treated depending on how they have behaved in previous interactions, retaining the option to occasionally apply punishment shifts the payouts to favor cooperators more than defectors.